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# SCOLOPOPHOROUS ORGANS IN THE PTEROTHORAX AND ABDOMEN OF GELASTOCORIS OCULATUS (FABRICIUS) (HEMIPTERA-HETEROPTERA)

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# No. 3 — Scolopophorous Organs in the Pterothorax and Abdomen of Gclastocoris oculatus (Fabricius) (Hemiptera-Heteroptera)

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# INTRODUCTION

Scolopophorous organs located on the body, as opposed to those on the appendages, are widely distributed among the orders of insects. These organs, which are especially common in immature insects, are also found in adult Lepidoptera, Hymenoptera, Odonata, Diptera, Homoptera, and Heteroptera (Eggers, '28). In some insects they may be highly complex, each organ consisting of a large number of strand-like sensilla. In this work there will be no attempt to review the extensive literature on these organs in insects other than the Heteroptera; however, it may be noted here that there have been numerous recent papers on their structure, most notably that of Gray ('60) on the electron microscopy of the scolopophorous organs of *Locusta*. Among the Heteroptera, scolopophorous organs have previously been reported only in representatives of the Hydrocorisae or totally aquatic bugs. Most earlier workers observed them only in the mesothorax; these paired mesothoracic organs were described in the Corixidae (Hagemann, '10; Eggers, '28; Wotzel, '33; Schaller, '51), Pleidae (Wefelscheid, '12; Eggers, '28; Wotzel, '33), Notonectidae (Wefelscheid, '12; Eggers, '28; Wotzel, '33), Naucoridae (Wefelscheid, '12; Eggers, '28; Wotzel, '33), Naucoridae (Wefelscheid, '12; Eggers, '28; Wotzel, '33) and Nepidae (Wotzel, '33). Similar organs on the metathorax were reported by Wotzel ('33) in the Naucoridae and Nepidae.

A recent survey by Larsén ('57) has revealed that in the Hydrocorisae scolopophorous organs occur not only in the mesothorax and metathorax but also in the first and sometimes the second abdominal segment. That author found discolopodial organs, each consisting of two sensilla, in the pterothoraxes and first abdominal segments of Nepa and Ranatra (Nepidae), Naucoris (Naucoridae), Aphelocheirus (Aphelocheiridae), Notonecta (Notonectidae), and Corixa (Corixidae). He also discovered monoscolopodial organs, each composed of a single sensillum, in the first abdominal segments of Corixa and Aphelocheirus and in the second abdominal segment of Aphelocheirus. Each segment containing scolopophorous organs possesses a pair of them, one lying on either side. Larsén criticized the theory, held by most previous workers, that the heteropteran scolopophorous organs are tympanal organs, and suggested that they may be equilibrium perceptors.

It now appears that scolopophorous organs in the Heteroptera are not limited to the Hydrocorisae. The present author has recently been studying the morphology of the shore-dwelling bug *Gelastocoris oculatus* (Fabricius), a representative of the family Gelastocoridae. This family is considered by China ('55) and other workers to have arisen as an early offshoot of the aneestral Hydrocorisae, and previous studies of the head (Parsons, '59), thorax (Parsons, '60a) and nervous system (Parsons, '60b) of *Gelastocoris* have supported this theory. *Gelastocoris* possesses discolopodial organs in the mesothorax, the metathorax, and the first abdominal segment, and a monoscolopodial organ. similar to that of *Aphelocheirus* or *Corixa*, in the first abdominal segment. In addition, a discolopodial organ occurs in the second abdominal segment; to the author's knowledge, this has not been previously observed in any other heteropteran.

# MATERIALS AND METHODS

Both the gross and the histological morphology of the gelastocorid scolopophorous organs were studied. Dissections were made upon a large number of adult *Gelastocoris* preserved in aqueous Bouin's, alcoholic Bouin's, Kahle's, F.A.A., or 10% formalin. The insects were dissected in 80% alcohol under a stereoscopic microscope. For histological study, seven gelastocorids were serially sectioned, at  $7\mu$ , by the paraffin method. These individuals were killed just after the adult moult, while their exoskeletons were still soft. They were preserved in aqueous or alcoholic Bouin's, F.A.A., or 10% formalin, and were prepared for sectioning by means of the Peterfi method. Both transverse and frontal sections, stained with Mallory's triple connective tissue stain, were employed.

# OBSERVATIONS

### GROSS MORPHOLOGY

The scolopophorous organs of *Gelastocoris* consist of one (as in the monoscolopodial organ<sup>1</sup> of the first abdominal segment) or two (as in the other organs) sensory sensilla or scolopodia, whose histological appearance will be described later. In the discolopodial organs the two sensilla are united into a common strand. The distal end of the scolopophorous organ may attach to a membrane on the body wall, as in the thorax and the first abdominal segment, or it may terminate upon an undifferentiated part of the exoskeleton, as in the second abdominal segment. Its proximal end, where it joins a sensory nerve, may be closely associated with a trachea (as in the thoracic organs) or with the endoskeleton (as in the first abdominal segment), or it may lie freely within the body cavity (as in the second abdominal segment). In the following discussion the scolopophorous organs of each segment will be considered separately.

Mesothoracic scolopophorous organ. The distal end of the mesothoracic organ attaches to a membrane which lies on the lateral mesothoracic body wall within the air space between the wings and the pleuron (Fig. 1, SM 2). Posteriorly and posterodorsally the membrane is bordered by the postalar bridge (B 2), which is formed by the union of the mesothoracic postnotum and

<sup>1</sup> The terminology in the present paper is that customarily used for the scolopophorous organs of Heteroptera; somewhat different terms have been used by other authors for other groups of insects.

epimeron. Ventrally it borders on the epimeron  $(E\ 2)$ , while anteriorly and anterodorsally it is continuous with the membrane of the forewing (FW). Just anterior to it lies the irregularly shaped subalare  $(S\ 2)$ . Larsén ('57) has described a similar connection of the sensory membrane with the subalar membrane



Fig. 1. Dorsolateral view of the right side of the pterothorax and the first two abdominal segments, showing the location of the sensory membranes of the discolopodial organs. The wings, the prothorax, and the posterior part of the abdomen have been cut off. Membranous areas are unstippled. X35.

in *Naucoris* and *Notonecta* and possibly in *Plea*; in those insects he thinks it possible, but not probable, that the motion of the wing may affect the organ. In the other Hydrocorisae examined by him the sensory membrane is separated from the wing membrane by a selerotized ring.

The sensory membrane in *Gelastocoris* is separated from the external opening of the metathoracic spiracle, which lies ventral and medial to it, by a longitudinal ridge on the inner surface of the epimeron. Larsén ('57) has described a similar separation of the membrane and the spiracle in *Nepa*, *Naucoris*, *Ranatra*, and *Aphelocheirus*; he found no such separation in *Notonecta* or *Corixa*.

The appearance of the sensory membrane (which Hamilton, '31, apparently mistook for the metathoracic spiracle in Nepa) is shown in Figure 2A. The point of attachment of the sense organ on the membrane appears externally as an indistinct,

slightly raised area. This represents the "Höcker" or "Trommelfellkörper" of previous authors. In some specimens a minute dark spot can be observed in the center of this raised area. This spot may be a very small sclerite, similar to those observed by Larsén ('57) in the sensory membranes of many Hydrocorisae.



Fig. 2. External appearance of the sensory membranes of the right side of the body. Heavy stippling indicates heavily sclerotized structures; light stippling indicates membranous regions. A, Mesothoracic sensory membrane. B, Metathoracic sensory membrane. C, First abdominal sensory membrane.

In the histological preparations, however, the raised area appeared more as a thickening of the membrane than as a definite sclerite. A few indistinct longitudinal folds may be observed in the membrane, but the folding is not as pronounced as in the mesothoracic sensory membranes of the Hydrocorisae described by Wotzel ('33) and Larsén ('57).

From its point of attachment on the membrane the mesothoracic scolopophorous organ (D 2) extends medially and somewhat posteriorly into the body cavity, beneath the postnotum (Figs. 3, 4). Proximally its base attaches to a trachea (DT 2); a similar connection of the base of the mesothoracic scolopophorous organ with the tracheal system has been noted by Larsén ('57) in the Hydrocorisae. Since the thoracic tracheal system of *Gelastocoris* shows some peculiarities, it will here be treated in some detail.



Fig. 3. Inner surface of the pterothorax and first two abdominal segments, right side, with the terga, wings, and muscles removed to reveal the scolopophorous organs, air sacs, and major tracheae. Membranous regions and cut edges are unstippled. Most of the tracheae have been cut off near their bases, and the distal parts of the air sacs have been removed. X40.

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The metathoracic spiracle (Fig. 3, SP) lies in the ventrolateral part of the body, at the boundary between the mesothorax and the metathorax. It was incorrectly termed the "mesothoracic spiracle" by both Brocher ('09) and Maulik ('16). Its external opening is overlapped and concealed by the extensive posterior lobe of the mesothoracic epimeron, which has been described in a previous paper (Parsons, '60a). A large, longitudinal lateral tracheal trunk (Figs. 3, 4, L) ("spiracular trunk trachea" of Hamilton, '31, and Presswalla and George, '35; ''Längstracheenstamm'' of Larsén, '57) joins the metathoracic spiracle with the more posterior first abdominal spiracle ("metathoracic spiracle"



Fig. 4. Dorsal view of the right side of the mesothorax and part of the metathorax, with wings, terga, and muscles removed. Part of the mesothoracic postalar bridge has been cut away to reveal the mesothoracic sensory membrane. The metathoracic spiracle and spiracular trachea are here concealed by the lateral tracheal trunk, which lies dorsal to them. Only the bases of the tracheae and air sacs are shown. Anterior region is shown at the left, posterior region at the right. X65.

of Brocher, '09, and Maulik, '16). Anteriorly, the lateral tracheal trunk extends medial to the mesothoracic pleural apophysis (Figs. 3, 4, P) and joins the *mesothoracic spiracle* (''prothoracic spiracle'' of Brocher, '09, and Maulik, '16), which lies between the prothorax and the mesothorax.

A very short spiracular trachea connects the metathoracic spiracle with the lateral tracheal trunk and also sends off tracheae to the mesothoracie leg and to the sternal area. From the lateral tracheal trunk, in the region where it unites with the spiracular trachea, arise two large air sacs (Figs. 3, 4, LA and MA) with very thin, folded walls. These saes are very delicate and are easily torn in dissections. Histological preparations reveal that they are composed of a folded layer of small cuboidal cells with a cuticular intima in which taenidia are either very faint or absent. The air sacs are broadly joined to the lateral tracheal trunk and do not arise from a constricted tracheal stalk as do the "Tracheenblasen" of many of the Hydrocorisae described by Larsén ('57). They were not observed in histological preparations of a nymph which had just moulted from the fourth to the fifth instar. These sacs were collapsed in all the specimens examined, and were never filled with air.

The lateral air sac (Figs. 3, 4, LA) arises just lateral to the metathoracic spiracle and extends forward between the body wall and the pleural apophysis, adhering closely to the latter. Anterior to the pleural apophysis it turns medially and becomes associated with one of the indirect flight muscles, M. mesonoti secundus, to which it sends many fine tracheoles. The lateral and medial walls of the sac are closely apposed. Air sacs with a similar position in the body have been described in many Hydrocorisae. The lateral air sac of Gelastocoris resembles the "bulbous trachea of the mesothorax" of Sphaerodema (Presswalla and George, '35) and is probably homologous with the "vordere Tracheenblase" described by Larsén ('57) in several aquatic bugs. In the majority of Hydrocorisae a lateral air sac lies close to the membrane of the mesothoracic scolopophorous organ; this has been observed in Notonecta (Wefelscheid, '12; Wotzel, '33; Larsén, '57), Naucoris (Wotzel, '33; Larsén, '57), Nepa (Wotzel, '33; Larsén, '57), Ranatra (Larsén, '57), and Belostoma (Larsén, '57). The association of the air sac and the sensory membrane is particularly close in the Corixidae (Hage-mann, '10; Eggers, '28; Wotzel, '33; Larsén, '57). In Gelastocoris, however, the lateral air sac lies at a considerably greater

distance from the sensory membrane than in any of the Hydrocorisae, and does not appear to be in any way associated with it. Larsén ('57) noted that in many of the aquatic bugs the lateral wall of the "vordere Tracheenblase" is more delicate than the medial wall. In *Gelastocoris*, however, no histological difference was noted between the two walls.

From the lateral tracheal trunk just posterior to the metathoraeic spiracle arises a second sac, the medial air sac (Figs. 3, 4, MA), which extends posteromedially between the mesothorax and the metathorax. It passes posterior to the ventral process of the second thoracic phragma. The medial air sac lies between and sends fine tracheoles to the tergal remotor muscle of the middle leg (M. noto-coxalis) and the tergal depressor muscle of the metathoracic trochanter (M. noto-trochanteralis). Like the lateral air sac, its walls are elosely apposed, especially in the region behind M. noto-coxalis; in dissections it appears as a broad dorso-ventral sheet separating that muscle from M. noto-trochanteralis. Medially it becomes associated with and sends fine tracheoles to the dorsal longitudinal flight muscles of the mesothorax, Mm. mesonoti primus et secundus.

Arising from the dorsal wall of the medial air sac, just where the latter joins the lateral tracheal trunk, is a medium-sized *dorsal trachea* (Figs. 3, 4, DT 2). This trachea extends dorsally and then turns medially, running along the region beneath the mesothoraeie postnotum and just anterior to the second thoracic phragma. From its base it sends off a fine trachea (WT 2) to the wing. The base of the mesothoraeic scolopophorous organ attaches to the posterior surface of this dorsal trachea, dorsal to the fine trachea which runs to the wing.

In both its position and its association with the mesothoracic scolopophorous organ, the dorsal trachea corresponds to the "Tracheenast" described by Wotzel ('33) in the mesothorax of *Notonecta*. Larsén ('57) has described a "hintere Tracheenblase," in the mesothoraxes of many Hydroeorisae, which arises from the "Längstracheenstamm" in the same region as does the dorsal trachea of *Gelastocoris*, and which, similarly, lies beneath the postnotum. In *Notonecta, Ranatra*, and *Nepa*, the mesothoraeic seolopophorous organ attaches to the tracheal stalk of this posterior air sac. These similarities make it appear probable that the dorsal trachea of *Gelastocoris*, although not an air sac. is homologous with the "hintere Tracheenblase" of the Hydrocorisae. In *Aphelocheirus aestivalis*, according to Larsén ('57). a "hintere Tracheenblase" is present in the nymph but appears in the adult as a trachea which lacks taenidia. This adult trachea lies in the same position as does the dorsal trachea of *Gelastocoris* and, similarly, serves as a point of attachment for the base of the mesothoracic scolopophorous organ.

The medial air sac of *Gelastocoris* resembles, in its position posterior to the ventral process of the second phragma and in its association with the dorsal longitudinal muscles of the mesothorax, the large trachea "Tr" of *Nepa* and *Ranatra* which is figured by Larsén ('57; his fig. 9). It also occupies the same position as the sac-like trachea which supplies the dorsal longitudinal muscles of *Notonecta* and which Larsén ('57) shows in his figure 25. The trachea to which the mesothoracic scolopophorous organ attaches (the dorsal trachea of *Gelastocoris* and the "hintere Tracheenblase" of *Notonecta*) arises from the base of the sac-like trachea of *Notonecta* and from the base of the medial air sac of *Gelastocoris*.

The mesothoracic scolopophorous organ is innervated by a branch of nervus mesothoracicus primus (Figs. 3, 4, N 2). As has been described in an earlier paper (Parsons, '60b), this first mesothoracie nerve sends a ramus to the dorsal longitudinal flight muscles, Mm. mesonoti primus et secundus. From the base of this ramus a branch extends posteriorly, passing medial to the promotor muscle of the middle leg, M. noto-trochantinalis, and then turning dorsolaterally, behind the remotor muscle of the leg, M. noto-coxalis. This nerve sends off a fine branch to the notum and then runs laterally, alongside (and often adhering to) the dorsal trachea. Near the base of the latter the nerve joins the proximal end of the scolopophorous organ, at the point at which the organ is attached to the posterior surface of the dorsal trachea (Figs. 3, 4, 11).

Metathoracic scolopophorous organ. Like the scolopophorous organ of the mesothorax, that of the metathorax attaches distally to a membrane (SM 3) lying within the subalar air space (Fig. 1). This membrane is bordered posteriorly by the metathoracic postnotum (PN 3) and ventrally by the epimeron (E 3). Anteriorly and dorsally it is continuous with the membrane of the hindwing (HW); just anterior to it lies the minute subalare (Fig. 2B, S). In belostomatids, Naucoris, and Notonecta the sensory membrane of the metathorax is similiarly continuous with the membrane of the wing; in Nepa and Ranatra, however, it is separated from the latter by a scherotized ring (Larsén, '57).

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Hamilton ('31) termed this membrane the "false spiracle" in *Nepa*. In *Aphelocheirus* the metathoracic scolopophorous organ lacks a sensory membrane (Larsén, '57).

In most specimens two minute dark spots on the membrane indicate the point of attachment of the scolopophorous organ. Whether or not these are definite sclerites could not be determined. As on the mesothoracic sensory membrane, the point of attachment of the sense organ appears as a small raised area.



Fig. 5. Dorsal view of the first two abdominal segments and the posterior part of the metathorax, right side, with the terga, the wings, and most of the muscles removed. Membranous areas and cut edges are unstippled. The distal portions of most tracheae and the dorsal parts of the dorsoventral muscles are ent off. Anterior region is shown at the left, posterior region at the right. X65.

Arranged around this point are many finely undulate longitudinal or concentric folds (Fig. 2B). The folds are more conspicuous in the metathoracic sensory membrane than in that of the mesothorax.

From the membrane the scolopophorous organ (Figs. 3, 5, D 3) runs medially and somewhat posteriorly to attach, like the mesothoracic organ, on a trachea (DT 3). Larsén ('57) reported a similar attachment of the base of the metathoracic sense organ on the tracheal system in most Hydrocorisae (the corixids are exceptions).

In the region of the metathoracic scolopophorous organ of Gelastocoris there are no air sacs; this is also true of the aquatic bugs (Larsén, '57). The first abdominal spiracle is surrounded by a sclerotized process of the abdomen which is fused with the metathoracic epimeron (Figs. 3, 5). A short, broad spiracular trachea (TI) joins the first abdominal spiracle with the lateral tracheal trunk from the metathoracic spiracle. It also sends two tracheae ventrally into the hindleg and, more dorsally, gives rise to a trachea which passes medially into the region between the thorax and the abdomen. From the dorsal part of the area in which the latter trachea, the lateral tracheal trunk, and the spiracular trachea come together, two smaller tracheae arise (Fig. 5). The larger and more medial of these, the dorsal trachea (DT)3), corresponds in its position to the dorsal trachea of the mesothorax; it extends dorsally and then medially, and supplies the remotor muscle of the metathoracic coxa, M. noto-coxalis. Like the mesothoracic dorsal trachea, it lies just beneath the posterior margin of the postnotum. Just lateral to the base of this metathoracic dorsal trachea arises a finer branch which extends anteriorly into the wing (Fig. 5, WT 3). It appears, in some specimens, as an offshoot of the base of the dorsal trachea, and is homologous with the fine mesothoracic trachea which runs from the dorsal trachea to the forewing.

The proximal end of the metathoracic scolopophorous organ attaches to the posterior part of the base of the dorsal trachea, and thus occupies the same position as does the mesothoracic sense organ. At this point it is innervated by a branch of *nervus metathoracicus primus* (Figs. 3, 5, N 3). The latter, as has been described in a previous paper (Parsons, '60b), consists of two main branches, one of which extends posteriorly and then laterally, around the promotor muscle of the hindleg, *M. noto-trochantinalis*. In the posteromedial part of the metathorax it sends a

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ramus to the tergum; it then passes between the remotor muscle of the leg and a dorsoventral muscle, *Mm. noto-coxalis et dorsoventralis*, respectively, and sends off a second ramus to the tergum. Laterally it becomes closely associated with the dorsal trachea and follows the latter ventrally to its base, where it innervates the metathoracic scolopophorous organ. *Scolopophorous organs of the first abdominal segment.* The

Scolopophorous organs of the first abdominal segment. The first abdominal segment possesses both a discolopodial organ (Fig. 5, D I) and a monoscolopodial organ (M I). Only the former attaches to a membrane; the latter ends in the connective tissues of the lateral sternal region (Fig. 8). Larsén ('57) has reported a similar situation in both Corixa and Aphelocheirus, and was the first author to observe the monoscolopodial organ in the Hydrocorisae. In the other aquatic bugs examined by him, only the discolopodial organ appears to be present in the first abdominal segment.

The location of the roughly circular sensory membrane (SM I)of the discolopodial organ is shown in Figures 1 and 5. It is almost completely surrounded by the tergal exoskeleton of the reduced first abdominal segment (I) (according to Larsén, '57, this sclerite corresponds to the postnota of the thoracic terga). Its anteromedial portion, however, is continuous with the membrane (Fig. 2C, IS) between the thoracic and abdominal terga. Larsén ('57) observed a similar connection of the sensory membrane with the intersegmental membrane in the first abdominal segments of all the Hydrocorisae examined by him, with the exception of Aphelocheirus. In the latter insect, the sensory membrane is completely surrounded by the exoskeleton.

The sensory membrane is somewhat recessed into the body cavity, and its surface curves inward more than do the membranes of the thoracic organs. The point of attachment of the scolopophorous organ appears as a small, somewhat raised area on the membrane (Fig. 2C). In most specimens this raised area contains one or two tiny dark spots similar to those seen on the metathoracic sensory membrane, and one individual shows a definite, irregularly shaped sclerite here. The sensory membrane of the first abdominal segment is approximately the same size as that of the metathorax and somewhat smaller than that of the mesothorax. Its folds are mostly radially arranged around the point of termination of the discolopodial organ. In the periphery of the membrane a few concentric folds are visible. From the membrane the discolopodial sense organ runs medially and ventrally, passing just posterior to the first abdominal spiracular trachea (Figs. 3, 5). It attaches to an irregularly shaped sclerite (Fig. 3, ST) which lies in the posterior part of the pericoxal membrane of the hindleg (CM 3). This sclerite is much more distinct in some individuals than in others. It is movably joined, by a membrane, to the sclerotized abdominal process which surrounds the first abdominal spiraele, and is probably abdominal in nature. On this sclerite originates the more anterior of two dorsoventral muscles (Fig. 5, MD) which lie on either side of the second abdominal spiracular trachea (T H). The base of the scolopophorous organ, and the nerve which innervates it, run in front of this anterior muscle.

The proximal part of the monoscolopodial organ of the first abdominal segment is joined with that of the discolopodial organ (Figs. 3, 5, 8). Larsén ('57) found a similar close connection of the basal ends of the two organs in *Corixa* and *Aphelocheirus*. The monoscolopodial organ is somewhat finer than the discolopodial organ and is difficult to trace. From its point of attachment on the irregularly shaped ventral sclerite it extends laterally, running parallel and ventral to the discolopodial organ (Fig. 5). Lateral to the first abdominal spiracular trachea it bends ventrally and ends, as in *Corixa* and *Aphelocheirus* (Larsén, '57), in the connective tissue ventral to the sensory membrane of the discolopodial organ (Fig. 8).

Both scolopophorous organs are innervated by a branch of *nervus abdominalis primus* (Figs. 3, 5, 8, NI). This branch, which also appears to innervate the muscle of the thoracic gland (Parsons, '60b), runs laterally into the region between the thorax and the abdomen and then extends ventrally into the area immediately anterior to the caudal part of the metathoracic pericoxal membrane. Here it runs anterior to the irregularly shaped sclerite of the latter membrane, and joins the combined bases of the two scolopophorous organs.

Scolopophorous organ of the second abdominal segment. The discolopodial organ of the second abdominal segment of Gelastocoris differs in several ways from the other discolopodial organs. Unlike the latter, it ends on unmodified exoskeleton rather than on a membrane. Its distal end, which appears to be somewhat broader than the rest of the organ, terminates in the hypodermis of the sternum of the second abdominal segment, medial to the region where the latter overlies the metathoracie coxa, and near the posterior border of the segment (Figs. 3, 5). From this point of attachment the organ  $(D \ II)$  extends anterolaterally and somewhat dorsally; in this respect it also differs from the more anterior scolopophorous organs, which extend medially from their distal attachments rather than laterally. It is very difficult to trace the course of the second abdominal scolopophorous organ, both in dissections and in histological preparations, since it runs through a large mass of connective tissue.

Unlike the other scolopophorous organs, that of the second abdominal segment is not necessarily attached proximally to any other structure. In some specimens its base was associated with a fine tracheal branch from the second abdominal spiracle; in many others, however, it lay free in the body cavity. None of the individuals examined showed any connection between the proximal end of the organ and the integument of the body wall.

The scolopophorous organ is innervated by a branch of *nervus* abdominalis sccundus (Figs. 3, 5, NII) in the lateral part of the body cavity, lateral to the second abdominal spiracle. This nerve passes ventrally between the second abdominal spiracular trachea and the more posterior of the two dorsoventral muscles which lie near that trachea. The nerve and the scolopophorous organ of this segment, unlike those of the preceding segments, form a sharp angle with each other. Also, unlike the nerves to the more anterior sense organs, the nerve supplying the organ of the second abdominal segment does not end at the base of the organ but branches and continues laterally into the side of the abdomen.

A scolopophorous organ has been described in the second abdominal segment of only one other heteropteran. Larsén ('55; '57) has reported a monoscolopodial organ, in the second abdominal segment of *Aphclochcirus*, which, like the discolopodial organ of *Gclastocoris*, attaches distally to the ventral body wall. It differs from the scolopophorous organ of *Gelastocoris*, however, in two major respects: it consists of one rather than two sensilla, and its basal end is always associated with a tracheal sac, of a peculiar structure, which lies close to the second abdominal spiracle in *Aphelocheirus*.

# HISTOLOGICAL OBSERVATIONS

In *Gelastocoris*, each *scolopophorous organ* or *scoloparium* consists of either one or two *sensilla* or *scolopodia*. In the discolopodial organs the two sensilla lie side by side, and the boundary between them is rarely distinguishable. The sensilla of all five scolopophorous organs show the same basic histological structure.

Histological preparations reveal that the gelastocorid sensilla are composed of three types of cells (Fig. 6): a distal *cap cell* (*CC*) (Snodgrass, '35; 'Deckzelle'' of German authors; possibly the ''attachment cell'' of Gray, '60), an intermediate *enveloping cell* (*EC*) (Snodgrass, '35; ''Hüllzelle'' of German authors),



Fig. 6. Frontal section through the right side of the mesothorax, showing the mesothoracic discolopodial organ and its relation to the dorsal trachea and sensory membrane (reconstructed from several consecutive serial sections). Sclerotized structures are shown in solid black. Lateral region is at the right, medial region at the left. X425.

and a proximal, basal sensory cell (SC) (Snodgrass, '35; ''Sinneszelle'' of German authors). Between the enveloping cell and the cap cell lies a spindle-shaped sensory rod or scolops (SL) (Snodgrass, '35; ''Stift'' of German authors; ''scolopale'' of Gray, '60). The appearance and position of these elements in the sensillum corresponds, in general, to the descriptions of previous authors (Eggers, '28; Wotzel, '33; Larsén, '57) who examined other Heteroptera by means of the light microscope.

#### PARSONS: SCOLOPOPHOROUS ORGANS

In the discolopodial organs of the mesothorax, metathorax, and first abdominal segment, the two cap cells of the paired sensilla attach to sensory membranes. In a few preparations the endings



Fig. 7. Detail of the point of attachment of the first abdominal discolopodial organ on its sensory membrane. Frontal section. X400.



Fig. 8. Cross section through the lateral part of the first abdominal segment, in the region of the discolopodial and monoscolopodial organs (reconstructed from several consecutive serial sections). Lateral region is shown at the left, medial region at the right, dorsal region at the top, ventral region at the bottom. X225.

of the two sensilla upon the membrane are distinct from one another; in most sections, however, the sensilla lie so closely together that only a single ending of the scolopophorous organ is evident (Fig. 7). There appears to be little, if any, increase in the number of hypodermal cells around the area of attachment. Although the point of attachment is not greatly differentiated, the cuticula of the membrane in this region usually appears somewhat thicker and more lightly stained than the surrounding cuticula, and is slightly raised above the level of the surrounding membranous folds.

The cap cell of the first abdominal monoscolopodial organ appears to branch into many fine processes in the ventral part of the abdominal body cavity, just beneath the membrane of the first abdominal discolopodial organ (Fig. 8). In this area, and throughout the abdomen, lie many large cells (LC) with deeply staining nuclei containing large chromatin granules. Their granular cytoplasm stains gray in Mallory's triple connective tissue stain and sometimes contains small vacuoles. These cells, which are spherical or oval in form, usually occur in clumps. The fine branches of the cap cell of the monoscolopodial organ seem to be continuous with the connective tissue (CT) in this region and to be closely associated with these clumps of large cells; they appear to end eventually in the hypodermis of the ventral body wall.

The discolopodial organ of the second abdominal segment also terminates in the hypodermis of the body wall. Unlike the more anterior discolopodial organs, however, it is not associated with a membrane and the exoskeleton overlying the point of attachment is not modified in any way. The two sensilla could be traced to their point of termination in approximately half of the sense organs examined histologically; one preparation (Fig. 9) shows a clear two-part separation of the sensilla in this region.



Fig. 9. Detail of the point of attachment of the second abdominal discolopodial organ in the hypodermis of the second abdominal sternite. X1000.

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In the sensilla of all five organs, the very elongate cap cells possess a fibrillar, lightly-staining cytoplasm and elongate nuclei (CN) which contain few chromatin granules of various sizes (Fig. 10). According to Eggers ('28), both the cap cell and the enveloping cell represent modified supporting cells. The position of the nucleus of the cap cell in *Gelastocoris* is extremely variable; this variation is evident not only among different individuals but between the scolopophorous organs of the two sides of one specimen, or between the two sensilla of a single scolopophorous organ. The nucleus may lie anywhere within the cell; it is, however, more commonly present in the proximal half than in the distal half of the latter. Larsén ('57) has pointed out this variation in the position of the nucleus in the cap cells of *Aphelocheirus*.



Fig. 10. Detail of part of the right mesothoracic discolopodial organ. Frontal section through the body, taken in the region of the scolops.

Proximal to the cap cells lie the elongate but shorter enveloping cells (Figs. 6, 10). Although Larsén ('57) reported a more alveolar, lighter-staining cytoplasm in the latter than in the former, the fibrillar cytoplasm of the enveloping cells stains considerably darker than that of the cap cells in *Gelastocoris*. The boundary between the cap and enveloping cells is not clear in any of the preparations; it lies somewhere at the level of the scolops. The elongate nucleus of the enveloping cell (EN) is located just proximal to the scolops. In the discolopodial organs the nuclei of the two enveloping cells lie at approximately the same level.

The scolops is a spindle-shaped body staining a deep red in Mallory's triple connective tissue stain. Its form is similar to that described in many Hydrocorisae by previous authors (Fig. 10). Cross sections through the scolops reveal that it is hollow, with a slender process running through its center from the proximal to the distal end. The two ends and the medial, somewhat indented central portion of the scolops are encircled by thickened rings. Between these rings the walls of the scolops are thinner and appear to be composed of five or six ribs which run parallel to the longitudinal axis of the scolops. This appearance of the scolops is in general agreement with the previous descriptions of Hagemann ('10; *Corixa*), Wefelscheid ('12; *Plea*), and Eggers ('28; *Plea* and Corixidae).

The proximal part of the scolops is surrounded, in most preparations, by a vacuolar space (Fig. 10) which is probably an artifact (Gray, '60). In the discolopodial organs, the scolopes of the two sensilla lie either side by side or one slightly distal to the other. The scolops of the monoscolopodial organ in the first abdominal segment is located just ventral to the scolopes of the discolopodial organ of that segment. The slender central process of the scolops continues proximally through the vacuolar space and the region of the enveloping cell, and appears to extend into the sensory cell area. This proximal strand (Fig. 10, A) represents the "Achsenfaden" of previous authors.

Gray's ('60) recent electron microscope study of the abdominal tympanal organ of Locusta has revealed much concerning the fine structure of the scolops. The latter, which he termed the "scolopale," is an intracellular, fibrous structure within a "scolopale cell." The "scolopale cell" may correspond to the enveloping cells of the present study, but this is uncertain; the electron microscope reveals more cells in the sensillum than does the light microscope, and their appearance is considerably different in Locusta and Gelastocoris. Gray confirmed the observation, made in the present study, that the walls of the scolops are composed of thickened rods; he further observed that these rods may branch. Fitting over the distal end of the "scolopale cell" is an extracellular, fibrous "scolopale cap." This cap, along with the merged distal ends of the "scolopale rods," probably corresponds to the distal thickened ring observed in the scolops of Gelastocoris. while the fusion of the proximal ends of the rods produces the most proximal ring. The electron microscope shows that the dendrite of the sensory cell ends within the base of the scolops, and from its point of termination a cilium projects distally into the "scolopale cap." This cilium probably corresponds to the slender central process observed in the scolops of Gelastocoris. Gray described a system of branching rootlets at the base of the cilium. These rootlets extend proximally, within the dendrite, nearly to the nucleus of the sensory cell; they probably represent the "Achsenfaden" of the present study.

In some preparations of *Gelastocoris* a distal process from the seolops could be observed running for a short distance through the region of the cap cells. Whether this process (the "Endfäden" of previous authors) extends to the distal end of the cap cells could not be determined; if so, it is much finer and more difficult to see distally than proximally. Eggers ('28) considered the seolopophorous organs of the Hydrocorisae to be "amphinematic," a term used for organs whose "Endfäden" extend all the way to the integument. Wotzel ('33), however, reported that the Hydrocorisae lack "Endfäden" and thus possess "mononematic" seolopophorous organs. Larsén ('57), although unable to trace the "Endfäden" to the end of the cap cells in most of his preparations of Hydrocorisae, believed them to be present in all. Gray's ('60) study, unfortunately, offers no hints as to the nature of the "Endfäden."

At the base of the sensillum lies a large sensory cell (Figs. 6, 11, SC) with granular, lightly-staining cytoplasm and a round nucleus containing few chromatin granules. In the discolopodial organs the sensory cells of the two sensilla lie close together and are surrounded by *supporting cells* (Fig. 11, SUP) ("akzessorische Zellen" or "Hüllzellen" of previous authors). The



Fig. 11. Detail of the base of the left mesothoracic discolopodial organ. Frontal section through the body. Anterior region is shown at the bottom, posterior region at the top. X975.

latter, which form a sort of capsule ("Hüllschicht" of Wotzel, '33) around the two sensory cells, are variable in size. They are smaller than the sensory cells and their nuclei are richer in chromatin. Both the sensory and the supporting cells are enclosed by a membrane which is continuous with the neurilemma of the nerve innervating the scolopophorous organ. The bases of the mesothoracic and metathoracie scolopophorous organs, which lie beside tracheae, are connected to the latter by fine processes from the supporting cells (Fig. 11), and the combined bases of the monoscolopodial and discolopodial organs in the first abdominal segment (Fig. 8, DM 1) are similarly attached to the sternum.

In two of the seven sectioned specimens, a fine nerve (Fig. 12, N) was observed coming off from the area of the sensory cells at the base of the metathoracic scolopophorous organ. This was clearly seen on both sides of one individual; in the second, which



Fig. 12. Detail of the base of the left metathoracic discolopodial organ, showing the slender nerve which arises from this region. Cross section through the body, taken posterior to the point at which the discolopodial organ attaches to its sensory membrane. Dorsal region is shown at the right, ventral region at the left, medial region at the top, lateral region at the bottom. X700.

was poorly preserved, it appears to be present on at least one side. The nerve, which is much more slender than the scolopophorous organ, leads to a large cell (C) which resembles, in its size and staining properties, the sensory cells of the sensilla.

Grouped around this cell are several smaller cells resembling the supporting cells at the base of the scolopophorous organ. Distal to the large cell the nerve sends slender branches through the connective tissues to the hypodermis in the region of the axillary cord (HA), posterior to the point of termination of the scolopophorous organ on its membrane. Wotzel ('33) observed a fibrous "Strang," associated with the metathoracie seolopophorous organs of Naucoris, which resembles this nerve in Gelastocoris and which contains a similar large and apparently sensory cell. In Naucoris the "Strang" appears to be considerably longer than the nerve of Gelastocoris and to run closer and more parallel to the scolopophorous organ. According to Wotzel, the processes at the distal end of the "Strang," which run to the hypodermis, end very close to the point of attachment of the scolopophorous organ. In Gelastocoris, the fine processes distal to the large cell appear to meet the integument at a point more distant from the termination of the scolopophorous organ.

In the first abdominal segment, the sensory cell of the monoscolopodial organ lies beside the two sensory cells of the discolopodial organ (Fig. 8). All three cells appear to be surrounded by a common layer of supporting cells and innervated by the same nerve. In many preparations a broad ligament was observed connecting the bases of the two scolopophorous organs with the irregularly shaped selerite of the posterior pericoxal membrane, which has been previously described. The monoscolopodial organ separates from the discolopodial organ at approximately the level of the nuclei of the enveloping cells.

The base of the discolopodial sense organ of the second abdominal segment, unlike that of the first segment, is not connected with the integument but lies free in the lateral part of the body eavity. In approximately half of the preparations in which the base of the organ could be observed clearly, it was not associated with any other structure in the body cavity; in the rest, it lay close beside a fine trachea from the second abdominal spiracle. Two of the latter specimens showed some attachment of the sensory cell area to the trachea by means of processes from the supporting cells; in the other preparations the basal part of the scolopophorous organ lay beside the trachea but was not attached to it. The occurrence of an attachment with a trachea appears to be quite variable; the two specimens in which a connection was observed showed this condition only on one side of the body.

### DISCUSSION

Previous studies on the anatomy of the head (Parsons, '59), the thorax (Parsons, '60a), and the nervous system (Parsons, '60b) of Gclastocoris have revealed a marked morphological similarity between this insect and the aquatic bugs or Hydrocorisae. These similarities support the theory of China ('55) and earlier workers that the Gelastocoridae and the aquatie Heteroptera are closely related phylogenetically. The presence of scolopophorous organs in Gelastocoris may provide additional morphological evidence in favor of this theory. Larsén ('57) has reported that similar organs have not yet been described in either the terrestrial bugs (Geocorisae) or the semi-aquatic forms (Amphibicorisae), and he was unable to find them in representatives of those two groups (further research may, of course, reveal their presence in the latter). The terrestrial and semi-aquatic bugs also lack mesothoracie air sacs, and in them the subalar air space is either absent or poorly developed (Larsén, '57); in Gclastocoris the air space is well developed, and air saes, although not inflated, are present.

The scolopophorous organs of *Gelastocoris* are, in general, very similar to those of the aquatic bugs. The position and appearance of the sensory membranes of the three anterior discolopodial organs, and their location within the subalar air space, are the same in *Gelastocoris* as in the Hydrocorisae. The basal attachment of the pterothoraeic organs upon tracheae, which has been noted in *Gelastocoris*, is also found in most aquatic bugs (Larsén, '57); similarly, in both groups the scolopophorous organs of the first abdominal segment attach proximally upon the sternum. Histologically, the sensilla of *Gelastocoris* are nearly identical with those of the Hydrocorisae as described by other authors. The monoscolopodial organ of the first abdominal segment of *Gelastocoris*, which has been previously reported in only two aquatic Heteroptera, *Corixa* and *Aphelocheirus*, is similar in all three of these inseets.

In two respects the scolopophorous organs of *Gelastocoris* differ from those of the aquatic bugs. First, the arrangements of the tracheal system in the mesothorax is unlike that of any of the Hydrocorisae thus far described. On the basis of the tracheal system and its relationship to the mesothoracie scolopophorous organ, Larsén ('57) grouped the Hydrocorisae into three main categories. In Ncpa, Ranatra, Bclostoma, Naucoris, and Notonecta, two air sacs are present, a "vordere" and a "hintere Tracheenblase"; the former lies close to the membrane of the scolopophorous organ, although it is not intimately associated with it. The lateral air sac of *Gelastocoris*, which is probably homologous with this "vordere Tracheenblase," does not lie anywhere near the membrane. Also, the probable homologue of the "hintere Tracheenblase," the dorsal trachea of *Gelastocoris*, is not developed into an air sac. In *Aphelocheirus*, which falls into Larsén's second category, air sacs are absent in the adults of at least one species (*A. aestivalis*) although they are present in the nymphs. *Gelastocoris*, on the other hand, shows air sacs in the adults but not in the nymphs. In *Corixa*, which forms Larsén's third category, an air sac corresponding to the "hintere Tracheenblase" of the other Hydrocorisae is intimately associated with the sensory membrane of the mesothoracie scolopophorous organ. No such intimate association of an air sac with the membrane was observed in *Gelastocoris*.

A second difference from the Hydrocorisae is the occurrence, in *Gelastocoris*, of discolopodial organs in the second abdominal segment. Only *Aphelocheirus* possesses seolopophorous organs in that segment, and in that insect, as has been previously noted, the organs are monoscolopodial and, unlike those of *Gelastocoris*, associated with a tracheal sac.

The function of the scolopophorous organs in the Hydrocorisae is, as yet, not definitely established. Larsén ('57) has presented a thorough and critical discussion of this problem, and the reader is referred to his paper for an extensive review of the literature on the subject. Most previous workers have considered the scolopophorous organs of the aquatic bugs to be tympanal hearing organs. This view is supported by the fact that in such groups as the Orthoptera, Lepidoptera, and Homoptera, sense organs resembling the pterothoracic and first abdominal discolopodial organs of the Heteroptera and, like them, attaching to membranes, are almost certainly sound perceptive. Also, many aquatic bugs such as the Corixidae, *Naucoris, Plea*, and *Ranatra* are known to stridulate (Larsén, '57).

Hagemann's ('10) experiments upon *Corixa* led him to conclude, with some reservations, that the corixid mesothoracic scolopophorous organ could perceive sound. Wefelscheid ('12; *Corixa* and *Plea*) and Schaller ('51; *Corixa*) also considered the mesothoracic organ to be a tympanal organ, and Wotzel ('33) believed the morphology of the scolopophorous organs in the Hydrocorisae to indicate that they are sound-perceiving structures. Eggers ('28), however, was uncertain as to whether they could be considered true tympanal organs.

Larsén ('57) has criticized the theory that the three anterior pairs of discolopodial organs in the Hydrocorisae are tympanal (he did not discuss the possible function of those scolopophorous organs which are not attached to membranes). He noted that an increase in the internal body pressure of a water bug causes the scolopophorous sensory membranes to bulge outwards, whereas other membranes, such as the subalar one, are unaffected by internal pressure changes. Such a reaction, he felt, indicates that the sensory membranes are not tympanal. He also pointed out that the membranes of the tympanal organs in other insects are tightly stretched, whereas those of the scolopophorous organs in the Hydrocorisae (with the exception of the corixid mesothoracic organ) are not tightly stretched but folded. Only in the mesothorax of the Corixidae, he believed, is there reason to presume that the scolopophorous organ has a sound perceptive function. The highly complex structure of the membrane of the corixid mesothoracic organ, which differs considerably from that of other Hydroeorisae, has been described by many authors (Hagemann, '10; Wefelscheid, '12; Eggers, '28; Wotzel, '33; Schaller, '51; Larsén, '57).

Larsén ('57) has proposed another possible function for the scolopophorous organs of the Hydrocorisae, that of orientation perception. He eited the facts that the sensory membranes of the three anterior pairs of organs all face externally onto a common subalar air space, and that they bulge outwards in response to an increased pressure from the internal body fluid. He further pointed out that the sensory membranes are bilaterally paired and arranged antero-posteriorly along the body. Larsén proposed that the pressure of the body fluid upon each of the membranes would vary according to the orientation of the body. He reasoned that those membranes lying at a lower level with respect to gravity would be subjected to more pressure from the internal body fluid than those higher up, and would, consequently, bulge further outwards, producing a greater tension upon the scolopophorous organs.

The discovery of scolopophorous organs in *Gelastocoris* does not shed much light upon the problem of their function. No experiments have been carried out to determine whether or not this insect is sensitive to sound. Stridulation has never been reported in *Gelastocoris*, and the author has never observed it in animals kept under laboratory conditions. However, stridulation has also not been demonstrated in some of the aquatic bugs possessing scolopophorous organs. Larsén's proposal that these organs may detect changes in the body's orientation appears, to the present author, to be somewhat questionable. Obviously, the problem of the function of the scolopophorous organs in *Gelastocoris*, as in the Hydrocorisae, cannot be resolved on the basis of morphology alone but requires, as Larsén ('57) has pointed out, further experimental work.

# SUMMARY

Paired scolopophorous organs, similar to those described by other authors in the aquatic Heteroptera (Hydrocorisae), are present in the mesothorax, the metathorax, and the first two abdominal segments of the shore-dwelling heteropteran Gelastocoris oculatus (Fabricius). The pterothoraeic and first abdominal segments contain discolopodial organs, each composed of two sensory sensilla, which attach to membranes located on the body wall within the subalar air space. The first abdominal segment also possesses a pair of monoscolopodial organs, terminating in the connective tissue in the ventral part of the abdomen, each of which consists of a single sensillum. The gross and histological morphology of these organs is similar to that of the scolopophorous organs of the Hydrocorisae, as described by previous authors. In addition, Gclastocoris possesses, in the second abdominal segment, a discolopodial organ which terminates on the sternum and is not associated with a membrane. Such an organ has not yet been reported in the Heteroptera. It differs from the second abdominal scolopophorous organ of Aphelocheirus since it contains two rather than one sensilla and is not necessarily associated with the tracheal system.

The presence of these organs in *Gelastocoris* supports the theory of China ('55) and other authors that the Gelastocoridae are closely related to the Hydroeorisae. Comparable organs appear to be absent in the semi-aquatic and terrestrial bugs.

The function of the scolopophorous organs of *Gelastocoris* is unclear. They may be involved with hearing or with orientation perception; previous authors have proposed these as two possible functions for the scolopophorous organs of the Hydrocorisae.

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#### EXPLANATION OF FIGURES

In the figures, the number "2" after an abbreviation indicates a mesothoracic structure, while a "3" indicates a metathoracic structure. The numerals "I" and "II" indicate structures of the first and second abdominal segments respectively.

The abbreviations used are as follows:

A-proximal strand of scolops	M – monoscolopodial organ
(''Achsenfaden'')	MA – medial air sac
B-postalar bridge	MD - dorsoventral muscles of second
C-large cell in nerve from base of	abdominal segment
metathoracic scolopophorous organ	MS – M. coxa-subalaris
CC-cap cell	N - nerve
CM – pericoxal membrane	$N \ 2$ – nervus mesothoracicus primus
CN – nucleus of cap cell	N 3 - nervus metathoracicus primus
CT - connective tissue	N I – nervus abdominalis primus
CX - coxal cavity	N II – nervus abdominalis secundus
D – discolopodial organ	NM – notum
DM I-combined bases of discolo-	P – pleural apophysis
podial and monoscolopodial organs	PE = prealar membrane
of the first abdominal segment	PV = narausidal membrane
DT – dorsal trachea	PX = postnotum
E – epimeron	R = postnottm
EC – enveloping cell	n – pieurai nuge
EN – nucleus of enveloping cell	S – subalare
ES – episternum	$SB \rightarrow subalar membrane$
$EX-\mathrm{exoskeleton}$	SC – sensory cell
F-furea	SL – scolops
FW – forewing	SM – sensory membrane of discolo-
H – hypodermis	podial organ
IIA - hypodermis in region of meta-	SP – metathoracic spiracle
thoracic axillary cord	ST-irregular sclerite in metathor-
HW – hindwing	acic pericoxal membrane
IS-intersegmental membrane be-	SUP - nucleus of supporting cell
tween thorax and abdomen	T – spiracular trachea
L – lateral tracheal trunk	TN – trochantin
LA – lateral air sac	WT – trachea to wing
LC-large cells in abdominal con-	I – tirst abdominal segment
nective tissue	11 – second abdominal segment

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